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BRIEF COMMUNICATION

Mineral content analysis in the rib cross-sections of *Homo sapiens* and *Pan troglodytes* and its implications for the study of Sts 14 costal remains

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Abstract

Introduction: From an evolutionary perspective, the ribcage has changed substantially in the subfamily Homininae. Among many other features, the amount of mineralized tissues of the rib cross-section at the midshaft could be informative about potential biomechanical changes during Homininae evolution. These changes would be related to the different loading stresses that each costal level has to deal with. Nevertheless, this knowledge remains hypothetical and has never been properly addressed.

Materials and Methods: This issue was assessed by analysing via micro-CT the internal rib anatomy of the complete sets of ribs belonging to ten *Homo sapiens* and ten *Pan troglodytes* adult individuals. Additionally, five fossil ribs of *Australopithecus africanus* Sts 14 (costal levels 5–9) were also included to evaluate similarities with the two tested extant species.

Results: The mineralized area of *P. troglodytes* rib cross-sections was higher than that of *H. sapiens*. However, its serial change along the rib sequence (1–12/13) was similar in both species. The mineralized area of the Sts 14 rib cross-sections was closer to *H. sapiens* than to *P. troglodytes* for costal levels 7–9 (Sts 14w) but not for levels 5 and 6, where it was distinct from both comparative samples.

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Discussion: The variation in the amount of mineralized tissues along the rib sequence in *H. sapiens* and *P. troglodytes* might indicate a common upper-lower thorax division probably linked to the insertions of the diaphragm. This variation is similar between ribs Sts 14w and the corresponding modern human costal levels, which could be potentially related to closer breathing kinematics in the lower thorax of Sts 14 and *H. sapiens*.

KEYWORDS
compartmentalization index, diaphragm, mineralized tissues, rib cross-section, thorax

1 | INTRODUCTION

Like many other anatomical structures, ribcage morphology has changed throughout the evolutionary history of Homininae (García-Martínez et al., 2018; Latimer et al., 2016), which may not be surprising given that this subfamily includes African great apes (genera *Gorilla* and *Pan*) and hominins (genera *Homo* and *Australopithecus*, among others) (Harrison, 2010). From a general perspective, the thorax of African great apes has been traditionally defined as "funnel-shaped", relatively narrower in its cranial part and wider in its caudal part. The so-called "barrel-shaped" thorax of *Homo sapiens* is relatively more volumetrically expanded in its cranial part and narrower in its caudal part (Bastir, García-Martínez, Williams, et al., 2017; Jellema et al., 1993; Latimer et al., 2016). Based on the study of external costal anatomy, Latimer et al. (2016) stated that the differences between both thoracic configurations could be linked to skeletal adaptations to specific modes of locomotion and breathing. Given the ability of the internal bone tissues to remodel during one's life to resist and adapt to the site-specific loading environment (Kivell, 2016), investigations of internal costal anatomy in Homininae could provide valuable information about potential biomechanical changes during evolution. These analyses involve sophisticated techniques that include non-destructive methods such as X-ray-based microtomography (micro-CT), which enable the study of internal costal anatomy without damaging the scarce material recovered from ossuaries or archeological and fossil sites (Kivell, 2016; Skinner et al., 2013).

By the application of these techniques, it has been suggested that the thoracolumbar spine has higher bone mineral density in adult African great apes compared to adult modern humans due to their skeletal adaptation to climbing, their different posture during ground locomotion (Cotter et al., 2011; Latimer et al., 2016) and the systemic gracility of the recent modern human skeleton (Chirchir et al., 2015; Ryan & Shaw, 2015). Since this could potentially affect the internal costal anatomy, rib cross-sections would also present a larger percentage of area occupied by mineralized tissues (% Min. Ar.) in adult African great apes, like *Pan troglodytes*, than in adult *H. sapiens*. Nevertheless, this premise has not been tested yet and remains as a hypothesis.

In this comparative framework, the ribcage configuration of *P. troglodytes* has been taken as a potential reference for that of *Australopithecus afarensis* (Schmid, 1983, 1991 contra Haile-Selassie et al., 2010). Even though the thorax of *P. troglodytes* could represent the primitive condition, with its retention in early hominins,

chimpanzees generally have 13 thoracic segments (ribs + vertebrae) in contrast to the 12 present in modern humans and the hominin fossil record (Schultz, 1961; Ward et al., 2017; Williams et al., 2016). Related to internal costal anatomy, it is not clear whether the % Min. Ar. of *Australopithecus* rib cross-sections might be closer to *P. troglodytes* or *H. sapiens* because of its apparently plastic locomotion and poorly known breathing kinematics (Schmid et al., 2013).

Therefore, this study aims to test for significant differences in the % Min. Ar. of the rib cross-sections at the midshaft in adult *P. troglodytes* and *H. sapiens* individuals. In this context, the best-preserved costal remains of *Australopithecus africanus* specimen Sts 14 were also analyzed. As the age estimated for this specimen varies approximately between 19 and 30 years old when the ossification of its epiphyses is compared to the standards of maturation of modern humans (Bonmatí et al., 2008), a comparison between the % Min. Ar. of the rib cross-sections of adult *H. sapiens* and *P. troglodytes* individuals and Sts 14 could help to determine not only the likely age of the latter but also biomechanical similarities between the tested species.

2 | MATERIALS AND METHODS

To carry out this study, we selected the complete sets of ribs of twenty individuals from the species *H. sapiens* and *P. troglodytes* that were non-pathological nor taphonomically altered. The ribs of ten potentially physically active medieval (8th–15th centuries) *H. sapiens* were included in the analysis (*N* = 120) and taken from the osteo-archeological collection belonging to the rural archeological site of Marialba de la Ribera (Candelas González et al., 2016), which is housed at the Universidad Autónoma de Madrid (UAM). These ribs were scanned by means of micro-CT at the Centro Nacional de Investigación sobre la Evolución Humana (CENIEH) facilities. We also scanned the ribs of ten contemporary *P. troglodytes* individuals (*N* = 130). While nine of them belong to the Department of Mammalogy at the American Museum of Natural History (AMNH) and were micro-CT scanned there, one individual of this species belongs to the Universidad de Alcalá (UAH) collection and was micro-CT scanned at the CENIEH. These samples were imaged using a V|Tome|X s 240 equipment (GE Sensing & Inspections Technologies) with the following specifications: resolution = 90 μm; kV = 110; uA = 100. All the studied *H. sapiens* and *P. troglodytes* individuals were considered adult based on the complete eruption of the third molars (Ubelaker, 1987;

Zihlman et al., 2007). Additional information on the taxonomy, sex and origin of the sample is provided in Table 1.

Furthermore, five ribs of *A. africanus* Sts 14 (Figure 1) (Ward et al., 2020), housed at the Ditsong National Museum of Natural History, were included. These costal remains, which have no evidence of taphonomic alterations, were micro-CT scanned at the South African Nuclear Energy Corporation (NECSA) using a 225 ST micro-CT scanner (Nikon Corporation) at 50 μm resolution with a voltage of 130 kV and current of 100 μA. Since the costal series of Sts 14 is incomplete and there is no consensus on the costal level of ribs Sts 14x, Sts 14y and Sts 14w (Figure 1), a hypothetical assessment was carried out based on the tubercle-iliocostal line distance (TID). This measurement is defined as the distance in a straight line from the center of the costal tubercle to the furthest extreme of the iliocostal insertion line (Franciscus & Churchill, 2002). As this distance increases from ribs 1 to 12, it is possible to sort ribs of the same individual from incomplete ribcages that are found commingled.

After completing these procedures, the final rib volumes were reconstructed and saved in DICOM format. All the rib cross-sections at the midshaft were extracted from these 3D digital rib models by Slicer 4.10.2 software (www.slicer.org; Fedorov et al., 2012) and

saved in TIFF format to be analyzed later by using Fiji software (Schindelin et al., 2012). The procedure for the extraction of the human and chimpanzee rib cross-sections started by drawing a tuberculo-ventral chord, which is a straight line between the ventral margin of the costal tubercle to the ventral-most point of the sternal end of the rib (Franciscus & Churchill, 2002). Then we calculated its bisection and extracted the cross-section at the point where that bisection crosses the rib corpus, which we considered as the midshaft (Figure 2). Given that the studied ribs of Sts 14 are not complete (Ward et al., 2020), we firstly had to estimate their length and then apply the method of rib cross-section extraction mentioned above (Figure 2). For this purpose, we used the great ape and human sample from Bastir, García-Martínez, Williams, et al. (2017) in order to calculate a linear regression between the tubercle-ventral chord (TVC) and the TID, getting an R^2 above 70% in all the cases (Table S1 and Figure S1). These regressions allowed us to estimate the approximate TVC using the TID from ribs 5–9 in Sts 14. We got TVC measurements of 134.22, 154.36, 167.19, 173.88 mm and 161.41 mm for ribs 5–9, respectively. This allowed us to estimate the approximate midshaft of Sts 14 ribs.

Lastly, the % Min. Ar. of each rib cross-section was calculated by the compartmentalization index (Comp. Index), which is the ratio

TABLE 1 Complementary information related to the tested *Homo sapiens* and *Pan troglodytes* individuals

ID	Collection	Species	Sex	State of captivity (only *Pan troglodytes*)
MARB09 70.1	Marialba de la Ribera (UAM)	*Homo sapiens*	Male	
MARB09 87	Marialba de la Ribera (UAM)	*Homo sapiens*	Female	
MARB09 102	Marialba de la Ribera (UAM)	*Homo sapiens*	Female	
MARB09 120.1	Marialba de la Ribera (UAM)	*Homo sapiens*	Male	
MARB09 143	Marialba de la Ribera (UAM)	*Homo sapiens*	Male	
MARB09 149	Marialba de la Ribera (UAM)	*Homo sapiens*	Female	
MARB09 150	Marialba de la Ribera (UAM)	*Homo sapiens*	Female	
MARB09 153	Marialba de la Ribera (UAM)	*Homo sapiens*	Female	
MARB09 178	Marialba de la Ribera (UAM)	*Homo sapiens*	Male	
MARB09 221	Marialba de la Ribera (UAM)	*Homo sapiens*	Female	
35,550	Department of Mammalogy (AMNH)	*Pan troglodytes*	Male	Captive (USA)
51,278	Department of Mammalogy (AMNH)	*Pan troglodytes schweinfurthii*	Male	Wild (Democratic Republic of the Congo)
51,379	Department of Mammalogy (AMNH)	*Pan troglodytes schweinfurthii*	Male	Wild (Democratic Republic of the Congo)
51,382	Department of Mammalogy (AMNH)	*Pan troglodytes schweinfurthii*	Male	Wild (Democratic Republic of the Congo)
51,394	Department of Mammalogy (AMNH)	*Pan troglodytes schweinfurthii*	Male	Wild (Democratic Republic of the Congo)
61,376	Department of Mammalogy (AMNH)	*Pan troglodytes schweinfurthii*	Female	Wild (Democratic Republic of the Congo)
89,351	Department of Mammalogy (AMNH)	*Pan troglodytes verus*	Female	Wild (Cote d'Ivoire)
167,343	Department of Mammalogy (AMNH)	*Pan troglodytes*	Female	Wild (Cameroon)
174,860	Department of Mammalogy (AMNH)	*Pan troglodytes*	Female	Wild (Equatorial Guinea)
PT1	Department of Biology (UAH)	*Pan troglodytes*	Female	Born wild somewhere, raised in captivity in Spain
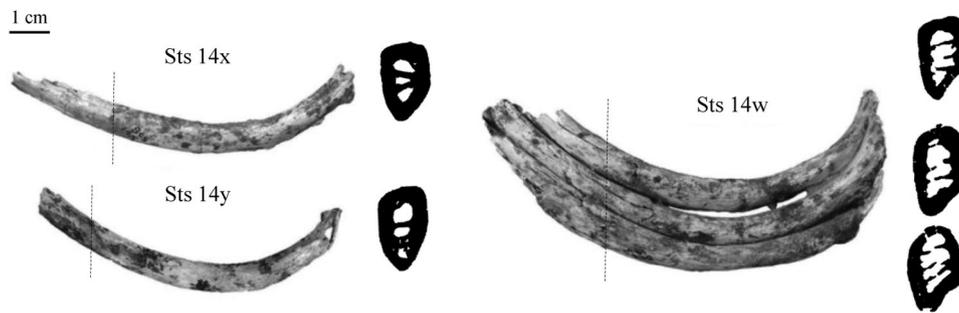
FIGURE 1 Studied ribs of *Australopithecus africanus* Sts 14 and their correspondent cross-sections extracted from an estimated midshaft, which is marked with a discontinuous line. While the designations Sts 14x and Sts 14y identify two independent ribs, Sts 14w names a block of three linked and serialized ribs (Ward et al., 2020)

FIGURE 2 Scheme for the extraction of the rib cross-section at the midshaft from a ninth rib of *Homo sapiens* and *Pan troglodytes*, as well as from Sts 14w. The selected ribs have been scaled so that they are depicted with the same size

Homo sapiens   *Pan troglodytes*   Sts 14
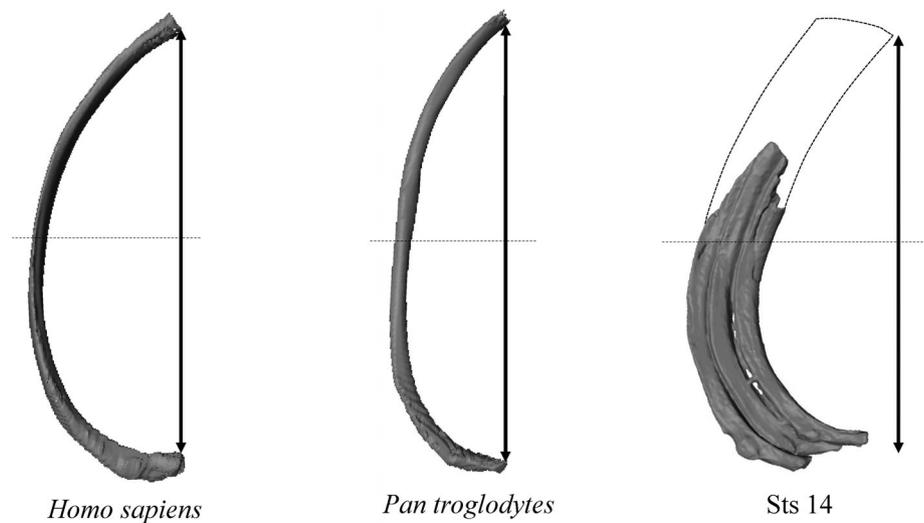
between its mineralized and non-mineralized areas (Cambra-Moo et al., 2014). A Kolmogorov–Smirnov test was used to test for normality of the data at each rib level, and significant differences between *H. sapiens* and *P. troglodytes* for each costal level were tested via a Student's t (ribs 12) or Mann–Whitney *U* test (ribs 1–11) (Table 2). All these statistical analyses were performed using Past 4.03 software (Hammer et al., 2001).

3 | RESULTS

As can be observed in Table 2 and Figure 3, the average Comp. Index of every costal level is significantly higher in *P. troglodytes* than in *H. sapiens* except for costal level 12. According to this result, it could be confirmed that rib cross-sections at the midshaft contain a higher % Min. Ar. in adult *P. troglodytes* than in adult *H. sapiens*. In addition, the sequential variation of the Comp. Index of both species follows a similar trend, which has a concave shape with the two maximum average values at the first and last rib and a minimum average value at the third costal level in *P. troglodytes* and the fifth one in *H. sapiens*.

Regarding *A. africanus* specimen Sts 14, the position of its ribs was determined to be from costal levels 5 to 9 based on the tubercle-

iliocostal line distance (TID). In particular, the shortest TID corresponds to rib Sts 14y (18.14 mm, costal level 5), followed by Sts 14x (23.38 mm, costal level 6) and finally Sts 14w (30.17, 32.95, and 33.51 mm, costal levels 7–9). The trend and Comp. Index of the cross-section at the midshaft of ribs Sts 14w (costal levels 7–9) are similar to the homologous of *H. sapiens* (Figure 3). However, the cross-sections at the midshaft of ribs Sts 14y (costal level 5) and Sts 14x (costal level 6) have an inverse trend and a Comp. Index that is over the 95% confidence interval in comparison with the homologous costal levels of *P. troglodytes* and *H. sapiens*.

4 | DISCUSSION

As mentioned by Cotter et al. (2011) and Latimer et al. (2016), the thoracolumbar spine has higher bone mineral density in African great apes compared to modern humans due to their different modes of locomotion. Since the ribcage could also be apparently affected, the main hypothesis of this investigation tests if rib cross-sections have a higher relative mineralized area (% Min. Ar.) in *P. troglodytes* than in *H. sapiens*. Our findings support this hypothesis at every costal level but level 12, which is not statistically different between humans and chimpanzees

TABLE 2 Statistical analyses of the Comp. Index in the common costal levels of *Homo sapiens* and *Pan troglodytes*

Comp. Index $\overline{X}$ ± SD	Rib 1	Rib 2	Rib 3	Rib 4	Rib 5	Rib 6	Rib 7	Rib 8	Rib 9	Rib 10	Rib 11	Rib 12	Rib 13
H. sapiens	3.68 ± 1.75	1.93 ± 0.71	1.78 ± 0.86	1.57 ± 0.58	1.47 ± 0.38	1,70 ± 0.49	1.81 ± 0.54	2.1 ± 1.03	2.28 ± 1.03	2.65 ± 0.91	2.95 ± 0.7	4.26 ± 1.73	–
P. troglodytes	6.59 ± 2.08	3.57 ± 1.17	2.98 ± 1.06	3.01 ± 0.73	3.24 ± 0.81	3.39 ± 1.11	3.37 ± 0.78	3.83 ± 1.39	3.97 ± 1.33	4.53 ± 1.18	5.27 ± 1.6	5.87 ± 2.03	7.94 ± 4.92
A. africanus Sts 14	–	–	–	–	7	4.5	2.5	2.9	3	–	–	–	–
Statistics													
K-S D	0.8	0.7	0.6	0.8	0.9	0.7	0.9	0.6	0.7	0.7	0.8	0.4	
p value	**0.001**	**0.007**	**0.03**	**0.0012**	**0**	**0.006**	**0**	**0.03**	**0.007**	**0.007**	**0.001**	0.3	
M-W U	10	9	19.5	3	1	7	1	14	14	8	5.5	–	
z	2.99	3.06	2.27	3.51	3.66	3.22	3.67	2.68	2.69	3.14	3.33	–	
p value	**0.003**	**0.002**	**0.023**	**0**	**0**	**0.001**	**0**	**0.007**	**0.007**	**0.002**	**0.001**	–	
Student's t	–	–	–	–	–	–	–	–	–	–	–	1.92	
p value	–	–	–	–	–	–	–	–	–	–	–	**0.07**	
95% CI H. sapiens	2.42–4.92	1.42–2.44	1.17–2.4	1.16–1.99	1.2–1.74	1.34–2.05	1.42–2.19	1.36–2.84	1.54–3.02	1.99–3.29	2.45–3.45	3.02–5.5	
95% CI P. troglodytes	5.1–8.12	2.73–4.4	2.22–3.74	2.49–3.52	2.66–3.82	2.6–4.18	2.81–3.93	2.84–4.82	3.02–4.92	3.69–5.38	4.13–6.42	4.43–7.32	4.42–11.47

Notes: The mean ($\overline{X}$), standard deviation (SD), and the 95% confidence interval (95% CI) are indicated as well as the performed tests with their correspondent statistical parameters (*p*-value in bold). The cross-sectional Comp. Index of the five ribs of *Australopithecus africanus* Sts 14 is also included.

FIGURE 3 Average rib cross-sectional Comp. Index per costal level in the whole set of ribs of the studied specimens of the species Homo sapiens and Pan troglodytes. The 95% confidence interval lines are accompanied by an image of the costal section with the extreme Comp. Index. The cross-sectional Comp. Index of the five ribs of Australopithecus africanus Sts 14 is also included
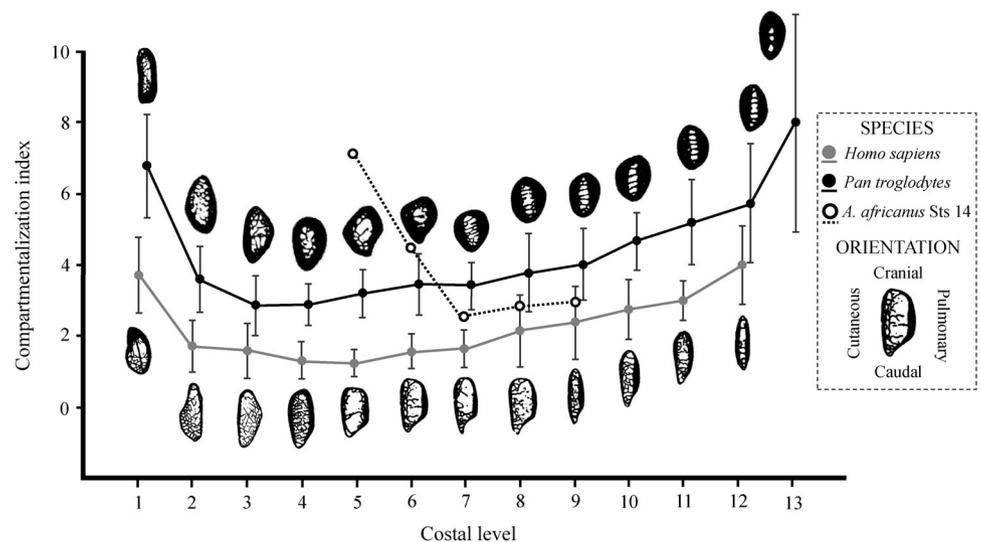
(Table 2, Figure 3). These results are generally in agreement with previous research that argues a systemic gracility of the recent modern human skeleton compared to apes, other hominins and even Upper Paleolithic H. sapiens (Chirchir et al., 2015; Ryan & Shaw, 2015; Ruff, 2018).

Focusing on the costal comparative analysis, the sequential variation of the Comp. Index in H. sapiens and P. troglodytes has a pronounced increment from rib 7 onwards (Figure 3), which matches with the position of the diaphragm insertions in both species (Gray, 1918; Schultz, 1930). Given that some authors consider the upper and lower thorax have different biomechanical functions due to the link that exists between the lower thorax and the diaphragm (Bastir, García-Martínez, Torres-Tamayo, et al., 2017; García-Martínez et al., 2016), a morpho-functional division between them might be potentially determined at the seventh costal level. Besides, the general trend of the curves in Figure 3 could be explained in accordance to Carter (1987), who theorized that bones exposed to higher mechanical stresses also present a higher % Min. Ar. By this premise, the highest average Comp. Index values seem to be related to those costal levels with the strongest muscular insertions. These muscular insertions are those led by the anterior and middle scalene on rib 1 and by the diaphragm on the most caudal costal levels (Gray, 1918).

With this in mind, our results could be hypothetically associated not only to the systemic gracility of the recent modern human skeleton but also to the different modes of breathing and locomotion in humans and chimpanzees. Firstly, the breathing of adult H. sapiens is eminently pulmonary in contrast with P. troglodytes, where it is eminently diaphragmatic (Gea, 2008). Then the bipedal locomotion of H. sapiens makes the weight of the head, neck, and arms pass through the spinal column, so it has no effect on chest wall biomechanics. On the contrary, the non-bipedal ground locomotion of P. troglodytes makes the weight of the head, neck, and upper thorax to pass through the upper ribs to the forelimbs (Casha et al., 2015). In addition, the vigorous arboreal activity of African great apes apparently affects the morphology and mobility of their axial skeleton (Cotter et al., 2011; Latimer et al., 2016). These facts make the ribs of P. troglodytes potentially more exposed to mechanical stresses than the ribs of H. sapiens, which may explain the differences between the Comp. Index

and, therefore, the % Min. Ar. of their rib cross-sections at the midshaft according to Carter (1987). Future studies should analyze how these biomechanical differences between both thoracic morphotypes could be connected to their different functionalities and 3D configurations (Bastir, García-Martínez, Williams, et al., 2017; Latimer et al., 2016).

The Comp. Index of the studied rib cross-sections of Sts 14 (Figure 3), whose serialization is in agreement with the consensus of previous research (Ward et al., 2020), shows departures in its serial change at costal levels 5 and 6 that might be related to its immature condition since skeletal growth was not complete in this young adult individual (Bonmatí et al., 2008). As reported by García-Martínez et al. (2017), the % Min. Ar. of the rib cross-section at the midshaft changes in association to ontogeny, being higher in immature than in mature stages of growth and development. In line with this premise, the Comp. Index of the studied Sts 14 rib cross-sections might be expected to be proportionally higher than it would be in an adult individual of the same species.

In addition, those Sts 14 ribs with a preserved tubercle region (Sts 14x and Sts 14w) show a nearly complete fusion of its articular epiphyseal plate (Bonmatí et al., 2008). According to the standards of maturation of modern humans (Scheuer & Black, 2000), Sts 14 might be considered a young adult as costal tubercle epiphyses fuse at the age of 18 in H. sapiens. Scheuer and Black (2000) also affirmed that rib head epiphyses fuse sequentially from the upper and lower extremes to the middle costal levels, completing costal maturation at the age of 22–25. Although the rib heads of the Sts 14 costal remains are generally damaged and not available for evaluation (Ward et al., 2020), the three ribs named Sts 14w could be considered more mature than ribs Sts 14x and Sts 14y because of the lower Comp. Index of their cross-sections and their assigned costal level (7–9). Taking into account that their maturation is not fully complete, the trend and the Comp. Index of ribs Sts 14w are already very similar to the corresponding costal levels of H. sapiens (Figure 3). Furthermore, previous publications have determined that Australopithecus specimens such as KSD-VP-1/1 present an antero-inferior declination of their lower ribs that is parallel to the condition described in humans and different from the African ape condition (Latimer et al., 2016). These features could indicate that breathing kinematics in the lower thorax of Australopithecus were closer to

H. sapiens than to *P. troglodytes*. Future studies should contrast the results of this research with new data taken from ribs of multiple *Australopithecus*, *H. sapiens* and *P. troglodytes* individuals with different states of maturity to test this hypothesis and describe not only the potential breathing kinematics of the *Australopithecus* lower thorax but also of its upper thorax.

To summarize the content of this article, the percentage of area occupied by mineralized tissues (% Min. Ar.) of the rib cross-section at the midshaft in adult *Pan troglodytes* individuals tends to be higher than in adult *Homo sapiens* individuals, which might relate to biomechanical differences in locomotion and breathing as well as to the systemic gracility of the recent modern human skeleton. Nevertheless, the serial change of the % Min. Ar. per costal level in both thoracic morphotypes is similar, which indicates that it is possible to define the division of the upper and lower thorax from rib 7 onwards attending to the insertions of the diaphragm. It is also important to state that, although *Australopithecus africanus* Sts 14 is considered a young adult, the breathing kinematics of its lower thorax could be more similar to *H. sapiens* than to *P. troglodytes* because of the Comp. Index of ribs Sts 14w and the human-like curvature of inferior ribs found in other well preserved *Australopithecus* specimens.

AUTHOR CONTRIBUTIONS

José María López-Rey Pérez: Conceptualization (equal); formal analysis (equal); investigation (equal); methodology (equal); visualization (equal); writing – original draft (lead). **Óscar Cambra-Moo:** Data curation (equal); resources (equal); supervision (equal); writing – original draft (supporting); writing – review and editing (equal). **Martín Armándo González:** Data curation (equal); resources (equal); writing – review and editing (supporting). **González Nieves Candelas:** Data curation (supporting); writing – review and editing (supporting). **Ángeles Sánchez-Andrés:** Data curation (equal); resources (equal); writing – review and editing (supporting). **Mirriam Tawane:** Data curation (equal); resources (equal); writing – review and editing (supporting). **Marine Cazenave:** Data curation (equal); resources (equal); writing – review and editing (supporting). **Scott A. Williams:** Data curation (equal); resources (equal); writing – review and editing (supporting). **Markus Bastir:** Writing – review and editing (supporting). **Daniel García-Martínez:** Conceptualization (equal); data curation (equal); formal analysis (equal); funding acquisition (lead); investigation (equal); methodology (equal); project administration (lead); resources (equal); software (equal); supervision (equal); validation (lead); visualization (equal); writing – original draft (supporting); writing – review and editing (equal).

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